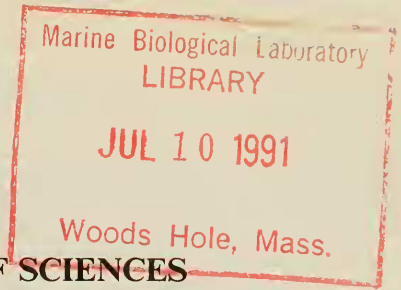


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REVIEW OF THE GRASSHOPPER GENERA *DRACOTETTIX* AND
LITOSCIRTUS (ORTHOPTERA: ROMALEIDAE),
WITH A DISCUSSION OF THEIR
ORIGINS AND LIFE HISTORIES

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ABSTRACT: The genera *Dracotettix* and *Litoscirtus* constitute the tribe Dracotettigini. The tribe is autochthonous in California, Nevada, and Baja California. Parsimony analysis indicates that *Litoscirtus* (southern) is the sister group of *Dracotettix* (northern), a finding consistent with the primarily tropical distribution of the family Romaleidae. The concealed male genitalia of all five species are similar and share characteristic laterally flared dorsal aedeagal valves.

Adult females of all Dracotettigini species can become reproductively dormant to pass the prolonged dry summers of California's Mediterranean-type climate. This ability in *D. monstrosus*, and perhaps other Dracotettigini, is geographically variable, as females from both mesic northern and some southern California localities remain reproductively active into the summer, but die soon after. In more xeric southern California populations, females enter reproductive dormancy in spring without having oviposited, become reproductively active in fall, mate, oviposit, and have adult life spans of up to 10 months. Interspecific timing of reproductive dormancy is also variable because of climatic differences at different locations. Thus, *L. insularis* from the central Baja California peninsula may be reproductively active during summer, when the area receives rain.

Litoscirtus platynotus new species, endemic to Baja California Norte, is described.

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INTRODUCTION

California supports a rich grasshopper fauna, including the 113 endemic species listed by Strohecker et al. (1968) and 11 endemic species described by Rentz and Weissman (1981, 1984). Most of the endemic species occur in the south and central coastal regions (Strohecker et al.

1968), which are characterized by a Mediterranean-type climate (Munz and Keck 1968).

Five species of *Dracotettix* Bruner and *Litoscirtus* Bruner are endemic to central and southern California, southwestern Nevada, and northern Baja California, Mexico. These grasshopper genera are biologically distinct from others in the region in having a robust body, a unique and

elaborate integumental sculpturing, a tendency for flightlessness, and an unusual life-history pattern that employs reproductive dormancy, apparently adaptive to a Mediterranean climate.

Grasshoppers of the thermally moderate Mediterranean climate of central and southern coastal California and northern Baja California Norte use at least eight different life-cycle patterns (Weissman and French 1980; Rentz and Weissman 1981). One of these patterns involves an adult period of reproductive dormancy. In the only detailed ecological study of a grasshopper utilizing such a strategy, Weissman and French (1980) found an average field adult longevity in *Trimerotropis occidentalis* (Bruner) of 70 days coupled with an ovipositional delay of up to 14 weeks after becoming adults. Adult female preovipositional mortality approached 50%. This strategy exposes mobile adults, not the sessile, more desiccation-prone eggs, to the hot, dry conditions of summer. Eggs are laid in the fall after the spring and summer dry period. Adults usually die with the advent of winter freezes, although in parts of coastal southern California they persist into the following spring (Uvarov 1966b; Rentz and Weissman 1981), living up to 10 months as adults.

Adult reproductive dormancy is widespread in insects (see references in Weissman and French 1980), especially in grasshoppers from areas with: (i) a Mediterranean climate (mild winter and prolonged summer drought); (ii) a tropical climate with a predictable drought exceeding several weeks duration, as in central Africa; and (iii) a harsh winter.

While reproductive dormancy in individual grasshopper species has been previously examined, no comparative study at a tribal level has been published. In this study we confirm Rentz and Weissman's (1981) findings of reproductive dormancy in *Dracotettix monstrosus* Bruner and report on the life-history strategies of four other species composing the tribe Dracotettigini of the family Romaleidae. Although the Dracotettigini are a small group and the species generally rare, these grasshoppers provide an interesting example of a group of insects that have evolved under a Californian Mediterranean climatic regime and show how flexible grasshopper life cycles can be.

The Romaleidae are predominately neotropical, but some species have radiated into temperate climates. Study of the life cycles of these

temperate species may help us to understand how tropical preadaptations, such as a reproductive dormancy, could allow these organisms reproductive flexibility in, and thus survival and colonization of, the temperate zone. The Dracotettigini evade dry and cold seasons differently than do the related *Taeniopoda eques* (Burmeister), which occurs at similar latitudes elsewhere in the United States Southwest and has a diapausing egg (Whitman and Orsak 1985), not a period of reproductive dormancy. The genus *Taeniopoda* apparently evolved in subtropical central Mexico (Rehn and Grant 1961) under a climatic regime quite different from that of northwestern Baja California Norte, where the Dracotettigini apparently originated.

Rehn and Grant (1959b, 1961) reviewed the Dracotettigini of America north of Mexico. They had little distributional data from Baja California and almost no biological information on the species. Herein we review the internal male genitalia of all four previously described taxa, describe a new species, give new distributional and ecological data for all taxa, and propose a phylogenetic history for the tribe. We then review seasonal collection records for all taxa and propose a generalized life-history scheme. Our proposed phylogeny and life-history strategy for the Dracotettigini indicate a center of evolutionary origin in southern California and northern Baja California Norte.

Most of the study specimens were collected by us and are deposited in the California Academy of Sciences (CAS). Additional specimens were kindly loaned by the CAS and the following museums: Academy of Natural Sciences of Philadelphia (ANSP), San Diego Natural History Museum (SDNHM), University of Michigan Museum of Zoology (UMMZ), the United States National Museum (USNM), and the E. L. Sleeper Collection, California State University, Long Beach (CSLB).

Geographical terminology used in this paper is mindful of, but not in complete concurrence with, Snelling (1987). Within the text, "Baja California" refers to the entire peninsula comprising Estado de Baja California ("Baja California Norte") and Estado de Baja California Sur ("Baja California Sur").

Dracotettix Bruner

Dracotettix Bruner, 1889:50 (type species *Dracotettix monstrosus* Bruner, 1889, by original designation); 1889:50; 1893:

TABLE 1. Diagnostic features of the *Dracotettix* and *Litoscirtus* species (see Fig. 1).

	<i>D. monstrosus</i>	<i>D. plutonius</i>	<i>D. newboldi</i>	<i>L. insularis</i>	<i>L. platynotus</i>
Anterior development of rostrum (width at eye/length)	greatly produced (0.96–1.44)	greatly produced (0.96–1.03)	weakly produced (0.95–0.99)	not produced (0.62–0.88)	not produced (0.50–0.62)
Wings surpass apex of hind femora	no	no	no	yes	yes
Fastigium rugose	yes	yes	no	no	no
Fastigium depressed at base	yes	no	no	no	no
Median pronotal crest (crest height/pron. width)	very high (0.31–0.45)	high (0.26–0.33)	high (0.24–0.35)	high (0.21–0.36)	low (0.08–0.18)
Prosternal tubercle	triangular	triangular	conical	conical	conical
Subgenital plate (male)	pointed	pointed	rounded	rounded	rounded
Number of antennal segments	16–18	16–18	22	22–23	23
Form of antennae	flattened	flattened	conical	conical	conical
Lateral margins of fastigium	bifurcate	bifurcate	entire	entire	entire

267; 1907:210, 226. Rehn and Hebard 1909:463. Hebard 1931:125. Rehn 1938:123–132. Roberts 1941:219, 239. Rehn and Grant 1959a:241–242; 1959b:131–135; 1961:178–181. Strohecker et al. 1968:22.

Roberts (1941) and Rehn and Grant (1959a) determined the phylogenetic position of *Dracotettix* based on phallic structures. Rehn and Grant (1959b, 1961) provided comprehensive taxonomic treatments of *Dracotettix* species. Subsequent references to the genus have appeared in Strohecker et al. (1968), Barnum (1964), and Rentz and Weissman (1981). *Dracotettix* was previously known from Baja California by the single species *D. newboldi* Hebard. We present new records for *D. newboldi* and *D. plutonius* Bruner, and the first records for *D. monstrosus* in Baja California. We compare the concealed male genitalia of all species because the dorsal aedeagal valves and the epiphallus are of diagnostic importance in the Dracotettigini (Rehn and Grant 1959a), and Rehn and Grant (1959a, b, 1961) did not compare the genitalia of all species in the tribe. Table 1 compares external diagnostic characters of the Dracotettigini.

Dracotettix monstrosus Bruner

(Figs. 1a, 2a, b)

Dracotettix monstrosus Bruner, 1889:50; 1907:226. Rehn and Hebard 1909:463; 1912:118. Rehn and Grant 1959b:143–156; 1961:186–189. Strohecker et al. 1968:22–23. Rentz and Weissman 1981:61–62.

Dracotettix californicus Bruner, 1907:226. Rehn and Hebard 1909:463.

CONCEALED MALE GENITALIA.—Specimens from Baja California (Fig. 2a, b) are similar to those described by Roberts (1941) and Rehn and Grant (1959a). Endophallus with dorsal aedeagal valves sclerotized, acute at apices, flaring subapically to form broad lateral plates, similar in shape to *D. plutonius*; ventral valves with simple lobes, sheath forming fleshy lobes, widely separated at ventral cleft. Epiphallus large with lophi enlarged at base and extending apically to acute points similar to that in *D. newboldi*; ancora large, extended inward and apically as bulbous lobes as in *D. newboldi*; bridge of epiphallus slightly convex at anterior margin when viewed dorsally, straighter and wider than in *D. newboldi*, more convex than in *D. plutonius*.

VARIATION.—Rehn and Grant (1959b, 1961) reported considerable size and shape variation in *D. monstrosus*, particularly in the body dimensions of females, the length of the tegmina in males, the height and shape of the pronotal crest, and the development and shape of the rostrum and fastigium in both sexes. Coloration is more variable in females than in males. The three males and one female reported here from Baja California do not deviate from this recognized variation. Body lengths of the three males range 22.6–24.6 mm, the tegmina range 10.7–11.7 mm. The rostra are greatly extended, and all four specimens have high pronotal crests similar to that in specimens from southern California.

Six specimens from Joshua Tree National Monument and two from nearby Whitewater

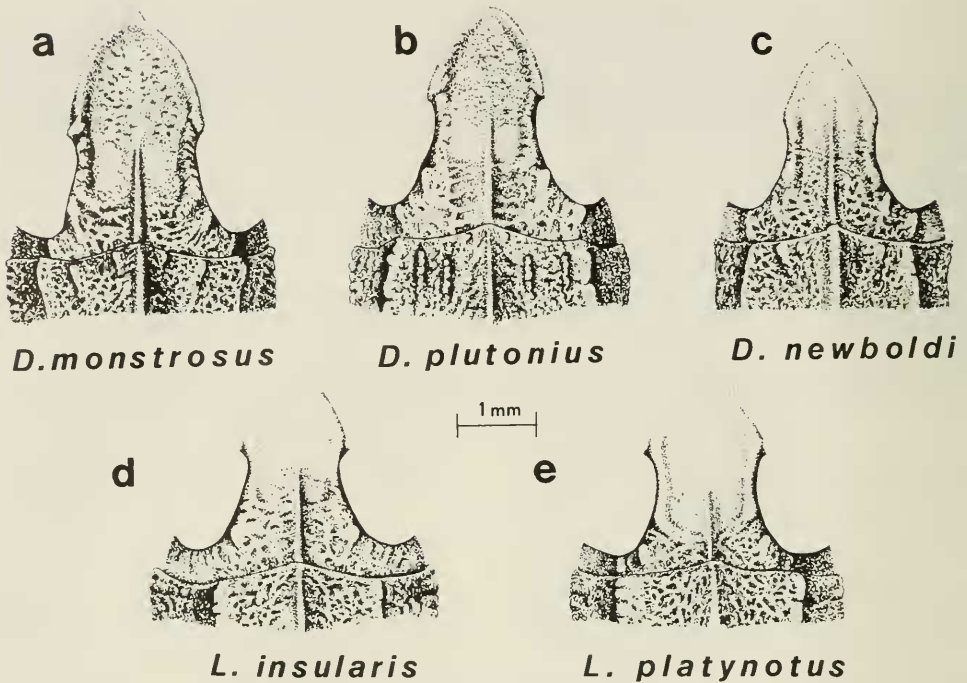


FIGURE 1. a-e. Dorsal views of adult male fastigia of Dracotettigini species (adult males). a, *Dracotettix monstrosus*, Table Mtn., Baja California Norte; b, *D. plutonius*, Panamint Range, California; c, *D. newboldi*, allotype; d, *Litoscirtus insularis*, topotype; e, *L. platynotus* holotype.

Canyon, Riverside County, California, represent the first records of *D. monstrosus* from desert areas. The six specimens from Joshua Tree National Monument were reported by Klud (1969) to be *D. plutonius*. All eight specimens are intermediate in four of six characters that Rehn and Grant (1959b, 1961) used to separate *D. monstrosus* and *D. plutonius*: metazonal crest height; fastigium length; fastigium profile; and extension of the rostrum. They are consistent with typical *D. monstrosus* for two: profile of metazonal crest; and shape of prosternal spine. These specimens are morphologically and geographically more consistent with typical *D. monstrosus* than with *D. plutonius*. We are unable to determine if the intermediacy results from genetic or environmental factors or both.

KARYOTYPE.— $2N \delta = 23$, all telocentric, two large, six medium, and three small autosomes, X medium sized. The karyotype of this species has been misinterpreted. Confusion has arisen because the meiotic bivalent configuration can affect the assignment of size class. Thus, Rentz and Weissman (1981) reported four large autosomes, but their figure 92 (p. 184) clearly shows

only two. In contrast, metaphase I pictured by Schroeter and Hewitt (1972) shows three large autosomes. To avoid misinterpretation, analysis should be performed on colchicine mitotic plates.

TYPE DATA.—*Dracotettix monstrosus*, lectotype, male, designated by Rehn and Hebard (1912), deposited in ANSP, type number H 83; Los Angeles, California, U.S.A. Not examined by us.

GEOGRAPHIC DISTRIBUTION.—Central and southern California Coast Ranges and inland mountains of southwestern California (Strohecker et al. 1968) and northwestern Baja California Norte (Fig. 3).

HABITAT.—Geophilous, preferring gravelly substrates where individuals are cryptic among small rocks. Rehn and Grant (1959b) reported *D. monstrosus* from near sea level to 2,400 m in California. *Dracotettix monstrosus* is generally associated with Californian chaparral or coastal sage scrub, but specimens from Joshua Tree National Monument were taken in pit-fall traps near juniper trees (Klud 1969) in a pinyon-juniper woodland.

PHENOLOGY.—Adults are known from Feb-

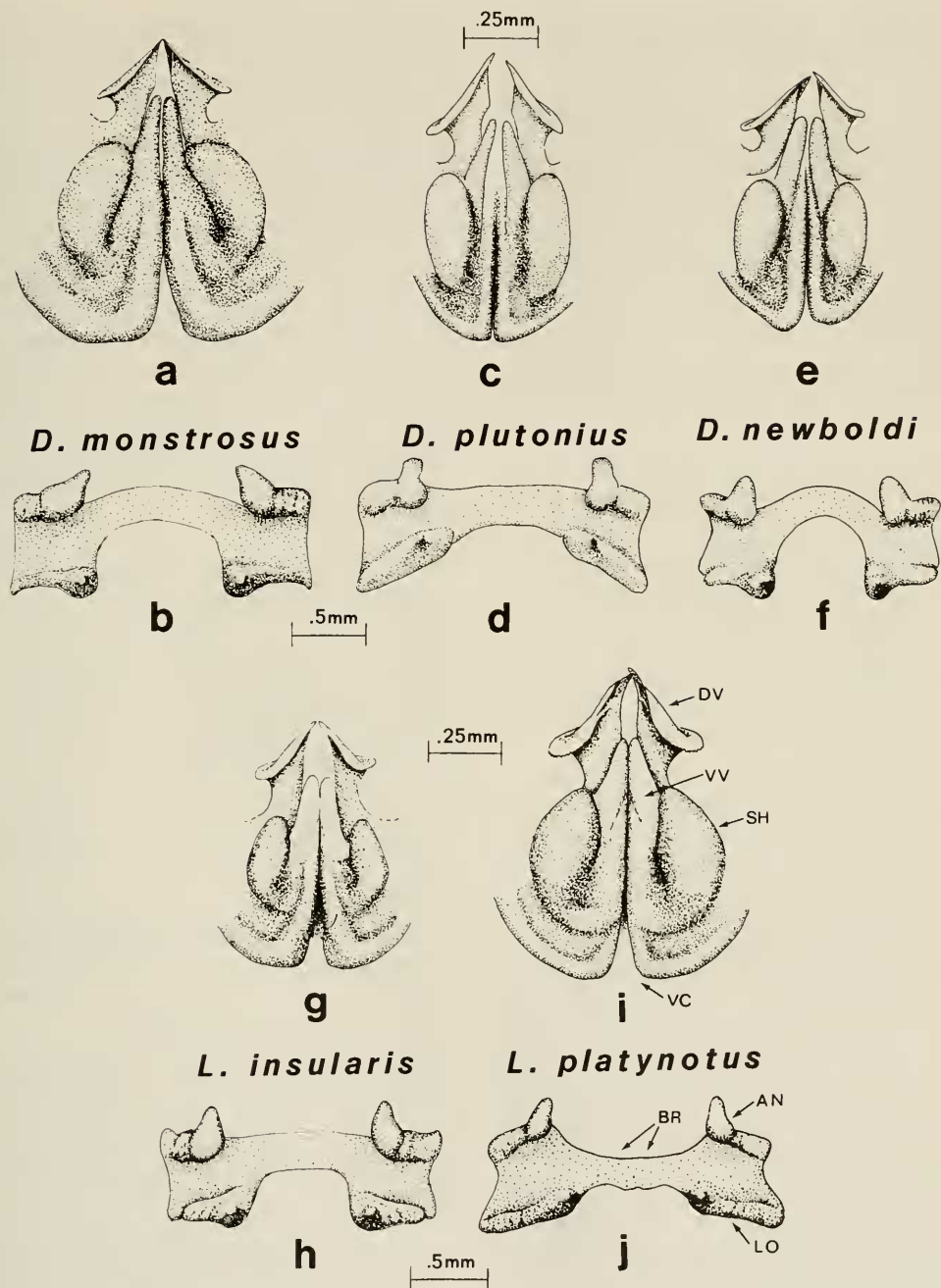


FIGURE 2. Concealed male genitalia. Posterior views of aedeagi (a, c, e, g, i): DV = dorsal valve, VV = ventral valve, SH = sheath, VC = ventral cleft. Dorsal views of epiphalli (b, d, f, h, j): AN = ancora, LO = lophus, BR = bridge. a, b, *D. monstrosus*, Table Mtn., Baja California Norte; c, d, *D. plutonius*, Panamint Range, California; e, f, *D. newboldi*, allotype; g, h, *L. insularis*, topotype; i, j, *L. platynotus*, holotype.

ruary to October, and immature stages from June to September. See discussion below on life histories.

NOTES.—One reproductively inactive adult female collected in southern California in July 1981 stridulated when held (see Strohecker et al. 1968 for similar observations). Stridulation was accomplished by a rubbing of the hind femora against the abdomen to produce a scraping sound. No other species of *Dracotettigini* has been reported to stridulate, but we have observed *Phrynotettix robustus* (Bruner), in the related tribe Phrynotettigini, to stridulate in a similar manner. Stridulation in the Romaleidae is discussed by Rehn and Grant (1959b:118).

SPECIMENS EXAMINED.—MEXICO. Baja California Norte: Table Mtn., 11.9 km E Rosarito (25 km S Tijuana), 20-IV-79 (D. K. Faulkner, 2 ♂, SDNHM); Valle de la Trinidad, Mesquite Springs, 16-III-59 (C. F. Harbison, 1 ♂, CAS); km 55 [from what city not indicated] on Mex. Hwy. 1, 6-V-62 (R. & A. R. Hardy, 1 ♀, CSLB). USA. California: Riverside Co.: Joshua Tree Natl. Mon., Lower Covington Flat (pit-fall trap), 9-IV-1961 (E. L. Sleeper, 1 ♀, CSLB), 5-IV-1966 (L. Garrick, 1 ♀, CSLB), 11-V-1968 (P. H. Klud, 1 ♀, CSLB), 25-X-1968 (R. A. Kramm, 1 ♀, CSLB), 12-IV-1969 (R. A. Kramm, 1 ♀, CSLB), 26-IV-1969 (E. L. Sleeper, 1 ♀, CSLB); Whitewater Canyon, 11-IV-1959 (J. C. Geest, 1 ♂, 1 ♀, CSLB).

Dracotettix newboldi Hebard

(Figs. 1c, 2e, f)

Dracotettix newboldi Hebard, 1931:125. Rehn and Grant 1959b: 135.

CONCEALED MALE GENITALIA (Fig. 2e, f).—Endophallus small relative to that in other *Dracotettix*: dorsal aedeagal valves sclerotized, acute at apices, flaring subapically forming broad plates with smooth margins; ventral valves simple, lightly sclerotized elongate lobes, relatively large; sheath forming fleshy lobes similar to that in *D. plutonius*; epiphallus small relative to that in other *Dracotettix*, with lophi enlarged at base and extended apically to acute points; ancora large, extended inward and apically to form bulbous lobes with flattened, pointed apices; bridge of epiphallus broad and strongly convex, more so than those in either *D. monstrosus* or *D. plutonius*.

VARIATION.—We examined too few specimens to assess variation. The adult female is similar to the holotype; the last instar female nymph from Todos Santos has a pronotal crest proportionately higher than those of the adult females. Late instar female nymphs of *D. monstrosus* and

Litoscirtus insularis Bruner also have pronotal crests that are proportionately higher than the crests of adults. This condition appears to be a tribal trait.

TYPE DATA.—Holotype, female, deposited in ANSP, type number 5496; Hamilton's Ranch, near Santo Domingo Mission, Baja California Norte, Mexico. Examined by us.

GEOGRAPHIC DISTRIBUTION.—Known only from the coastal plain region of Baja California Norte (Fig. 3).

HABITAT.—Fog-influenced coastal plains and foothills of Baja California Norte. The adult female that we found was on gravelly soil among *Agave*, iceplant, cacti, and *Frankenia*, on a broad fog-desert plateau some 2.5 km from the sea.

PHENOLOGY.—Adults are known from February and July; one last instar nymph was collected in March.

SPECIMENS EXAMINED.—MEXICO. Baja California Norte: Hamilton's Ranch (near Colonia Guerrero), 14-17-II-30 (Newbold, Morris, 1 ♂, 1 ♀, allotype and holotype, ANSP); Santo Tomas, 32 km S, 3-III-38 (Michelbacher, Ross, 1 last instar ♀, CAS); El Rosario, 4.5 km N, 9-VII-78 (D. B. Weissman, D. C. Lightfoot, 1 ♀, CAS).

Dracotettix plutonius Bruner

(Figs. 1b, 2c, d)

Dracotettix plutonius Bruner, 1893:267; 1907:226-227. Rehn and Hebard 1909:163. Rehn and Grant 1959a:241-242; 1959b:135-143; 1961:181-184. Barnum 1964:32-33. Strohecker et al. 1968:23.

This species was discussed extensively by Rehn and Grant (1959b, 1961) and does not occur in Baja California. The female spermatheca was figured by Rehn and Grant (1959a).

CONCEALED MALE GENITALIA (Fig. 2c, d; see also Rehn and Grant 1959a).—Endophallus similar in form to that in *D. newboldi*, dorsal aedeagal valves similar in shape to that in *D. monstrosus* and *D. newboldi*, but larger and more elongate, ventral valves and sheath form fleshy lobes, similar to that in *D. monstrosus* and *D. newboldi*; epiphallus with basal portion of lophi extended posteriorly as a narrow ridge; base of ancora broad, apices flattened and extended anteriorly, broadly rounded; bridge of epiphallus broader than that in *D. monstrosus* or *D. newboldi*, anterior margin almost straight.

VARIATION.—Rehn and Grant (1959b, 1961) discussed the range of morphological and color variation in *D. plutonius*, which is similar to that found in *D. monstrosus* but not as broad.

TYPE DATA.—Lectotype, male, designated by Rehn and Hebard (1912), deposited in USNM, type number 5496; Panamint Valley, Inyo County, California, U.S.A. Examined by us.

GEOGRAPHIC DISTRIBUTION.—Mountain ranges of the northern Mojave Desert, including the Panamint and Argus ranges, California, and the Mine Mountains at the Nevada Test Site, Nevada (Fig. 3).

HABITAT.—Barnum (1964:33) reported five individuals of *D. plutonius* from sagebrush (*Artemisia tridentata* Nutt.) and concluded that the species “undoubtedly feeds” on sagebrush. At Wild Rose Canyon, in the Panamint Range, we found individuals of *D. plutonius* on gravelly soil among grasses and forbs in an area between the creosotebush (*Larrea tridentata* (DC) Cov.) and pinyon pine zones. The vegetation was dominated by the shrubs box-thorn (*Lycium andersonii* Gray), blackbrush (*Coleogyne ramosissima* Torr.) and horse-brush (*Tetradymia spinosa* H. & A.), but no sagebrush was in the immediate area. We believe that *D. plutonius*, like other Dracotettigini, is primarily a geophilous species on gravelly soil, but individuals do climb onto shrubs, as Barnum (1964) observed, where they are equally well camouflaged as on gravel.

PHENOLOGY.—Adults are known from March through May, and in September. No nymphs have been found.

SPECIMENS EXAMINED.—USA. California: Inyo Co.: Panamint Range, Wild Rose Canyon, 1,550 m, 31-III-81 (D. C. Lightfoot, J. E. Price, 2 ♂, 2 ♀, CAS).

Litoscirtus Bruner

Litoscirtus Bruner, 1907: 210, 231 (type species *Litoscirtus insularis* Bruner, 1907, by monotypy; from a series of five syntypes from Cedros Island, Baja California, and one specimen erroneously labeled Central America [see Rehn and Grant 1959b]). Hebard 1923:326; 1931:124. Rehn 1938: 124–130. Rehn and Grant 1959b:127–129.

Hebard (1923, 1931) reported *L. insularis* from Turtle Bay on the Baja California peninsula adjacent to Cedros Island and from the Sierra San Pedro Martir, about 200 km to the north (the latter actually represents a record of the new species, *L. platynotus*). From the few specimens taken at the above localities, Rehn (1938) compared the external morphologies of *Dracotettix* and *Litoscirtus*, and Rehn and Grant (1959b) presented a comprehensive description of *Litoscirtus*. Since these works, *Litoscirtus* has appeared



FIGURE 3. Distribution of *Dracotettix* and *Litoscirtus* species in the southwestern United States and Baja California, Mexico.

in the literature only in reference to *Dracotettix* (Rehn and Grant 1961). Adults of both sexes of both *Litoscirtus* species fly well, in contrast to *Dracotettix monstrosus* and *D. plutonius*, where adults of neither sex can fly. We observed one living female *D. newboldi* that could not fly, but we have not observed a living male. Because of the short wings, we do not believe that males of this species can fly.

Litoscirtus insularis Bruner

(Figs. 1d, 2g, h, 4a, c)

Litoscirtus insularis Bruner, 1907:231. Hebard 1923:336; 1931: 124. Rehn and Grant 1959b:129–131.

All specimens we examined correspond with the description of Rehn and Grant (1959b). Hebard (1931) reported a single male *L. insularis* from the western slopes of the Sierra San Pedro Martir, Baja California. After examining that specimen, we conclude that it belongs to the new species *L. platynotus*. Males of the genus *Litoscirtus* were unknown before Hebard's report. He did note (Hebard 1931:124) that the male specimen “agrees closely with the female [*L. insularis*, Cedros Island], differing in being considerably smaller with pronotal cristation lower and

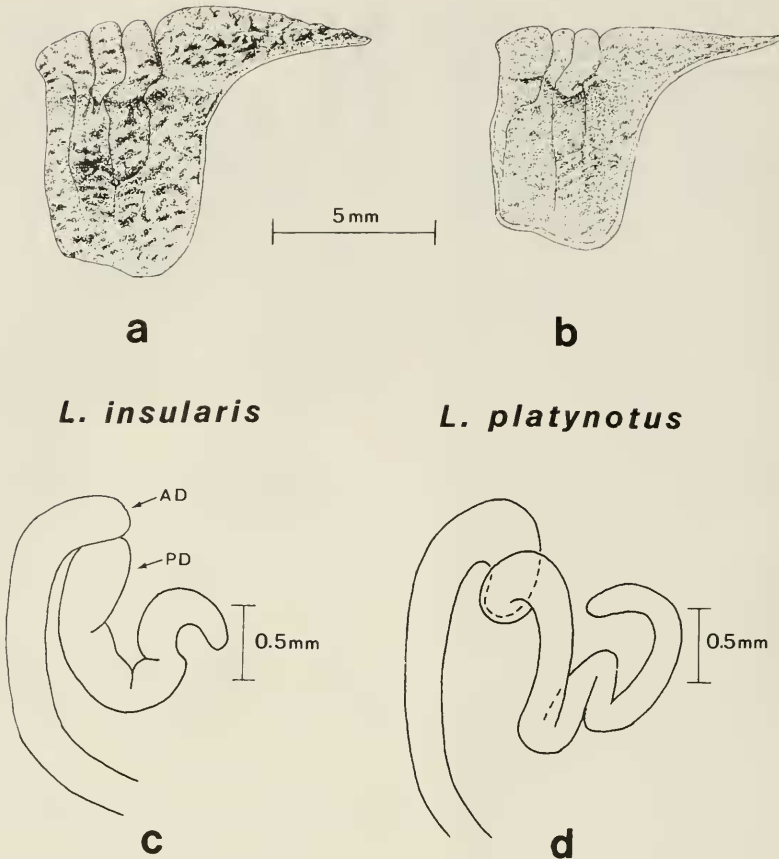


FIGURE 4. a, b. Lateral views of *Litoscirtus pronota* (females). a, *L. insularis*, toptype; b, *L. platynotus*, paratype. c, d. Lateral views of female spermathecae: AD = apical diverticulum, PD = preapical diverticulum. c, *L. insularis*, toptype; d, *L. platynotus*, paratype.

less incised." The height of the pronotal crest is actually proportionately similar in male and female specimens of *L. insularis* (Table 2).

CONCEALED MALE GENITALIA (Fig. 2g, h).—Endophallus small relative to that of other *Dracotettigini*, with dorsal aedeagal valves sclerotized and short, acute at apices, and flaring subapically to form broad lateral subapical plates, margins weakly serrate at apices, similar in shape to that in *Dracotettix* species; ventral valves simple, lightly sclerotized elongate lobes, sheath forming small fleshy lobes not reaching ventral cleft, proportionately smaller than *Dracotettix* species, and absolutely and proportionately much smaller than that in *L. platynotus*. Epiphallus with lophi enlarged at base, proportionately broader than in *L. platynotus*, and extended apically to acute points; ancora extended inward and apically to form bulbous lobes, proportionately

broader than in *platynotus*; bridge of epiphallus broad throughout and slightly convex when viewed from above, similar to that in *Dracotettix* species.

FEMALE SPERMATHECA.—Apical diverticulum present but poorly developed, evident only before the constriction to the preapical diverticulum (Fig. 4c); preapical diverticulum short and S-shaped.

VARIATION.—Little morphological variation is evident in *L. insularis* over its limited geographic range (Table 2). The male and female specimens from Natividad Island are the smallest known specimens of each sex. The shape and height of the pronotal crest vary little. Pronotal crest shape varies in the size and angle of cuts by the three sulci, and consequently, the angles of the lobes on the prozona. The male from Natividad Island had the highest pronotal crest of all males ex-

TABLE 2. Measurements (mm) of adult male and female *Litoscirtus* species.

	Body length*	Pronotum length	Pronotum width	Pronotal crest height**	Tegminal length
Males					
<i>insularis</i> (n = 9)	33.6–34.9	8.0–8.7	4.9–5.9	1.2–1.8	19.3–22.2
<i>platynotus</i> (n = 2)	32.9–33.1	7.2–8.6	4.9–5.2	0.4–0.8	19.9–20.7
Females					
<i>insularis</i> (n = 12)	41.8–46.4	10.3–12.3	7.0–8.2	1.6–2.4	31.1–35.4
<i>platynotus</i> (n = 3)	37.9–40.5	9.4–10.6	6.1–7.5	0.5–1.2	28.4–30.6

* Rostrum to apex of tegmina.

** Lateral carinae to apex of median metazonal crest when viewed laterally.

amined. The shape of the fastigium and rostrum varies little. Coloration varies somewhat, but not to the extent found in *D. monstrosus*. Most individuals have a dark gray-brown base color, contrastingly marked with light and dark gray. Some individuals have a reddish-brown base color, with light and dark reddish-brown markings. The tegmina are generally uniform gray-brown, with several large dark spots and light spots in the cubital region, varying to that in which individuals have the principal veins darkened with numerous small spots also present. Reddish-brown individuals have the same type of tegminal pattern. The entire tegmina of the two specimens from Natividad Island are heavily patterned with dark spots and light spots. Hind tibial color varies from uniform gray or uniform brown to red with gray mottling on the external face. Most individuals from Cedros and Natividad islands had gray hind tibiae, except for two males that had red hind tibiae. In contrast, all individuals from the Baja California peninsula had brown hind tibiae.

KARYOTYPE.— $2N \delta = 23$, all telocentric, two large, six medium, and three small autosomes, X medium sized. Three males collected on Cedros Island in early July had numerous meiotic divisions.

TYPE DATA.—Lectotype, male, designated by Rehn and Grant (1959b), deposited in USNM, type number 64,686; Cedros Island, Baja California Norte, Mexico. Not examined by us.

GEOGRAPHIC DISTRIBUTION.—Known only from the central west coast of Baja California in the vicinity of the Sierra Vizcaino and adjacent offshore islands, Cedros and Natividad (Fig. 3).

HABITAT.—From low coastal fog desert to high-elevation chaparral and pine forests (Cedros Island), from sea level to 1,300 m. This species occurs on open rocky soil, but is not associated

with any particular vegetation type. When we sampled Cedros Island in July 1983, *L. insularis* was most abundant at high elevations, but in April 1983, the species was common at both high and low elevations (D. K. Faulkner, pers. comm.). On the Baja California peninsula, *L. insularis* occurs in the Sierra Vizcaino and along the adjacent coastline. This region is characterized by Vizcaino sarcophyllus desert scrub (Wiggins 1980) on rocky, hilly terrain.

PHENOLOGY.—Adults are known from February through August. Late instar nymphs are known from March, April, and early July.

SPECIMENS EXAMINED.—MEXICO. **Baja California Norte:** Cedros Island: Grand Canyon, 8-IV-23 (G. D. Hanna, 1 ♀, CAS); 15-VII-39 (L. L. Walker, 1 ♀, SDNHM); El Pueblo, 12-IV-83 (D. K. Faulkner, 3 ♂, 1 ♀, 3 nymphs, SDNHM); Cerro de Cedros, 3-IV-83 (D. K. Faulkner, 1 ♀, SDNHM); Cerro de Cedros, 50–1,300 m, 28-VI-83 (D. K. Faulkner, V. F. Lee, D. C. Lightfoot, D. B. Weissman, 12 ♂, 9 ♀, CAS); Pico Gill, 30-VI-83 (D. K. Faulkner, V. F. Lee, D. C. Lightfoot, D. B. Weissman, 3 ♂, 3 ♀, CAS). **Baja California Sur:** Turtle Bay, 24-IV-16 (U.S. Fish Comm., 1 ♀, CAS); Scammon Laguna 19–23-VII-39 (L. I. Walker, 1 ♀, CAS); Picachos de Santa Clara, 27°07'N, 113°37'W, 350 m, 3-II-73 (R. Moran, 1 ♀, UMMZ); San Andres, 5 km SE, 27°14'N, 114°22'W, 65 m, 5-II-73 (R. Moran, 1 ♀, UMMZ). Natividad Island, 1 km N lighthouse, 13-VII-83 (D. K. Faulkner, V. F. Lee, D. C. Lightfoot, 1 ♂, 1 ♀, CAS).

Litoscirtus platynotus new species

(Figs. 1e, 2i, j, 4b, d)

This species is distinct from *L. insularis* primarily in the non-overlapping pronotal crest height measurements, disproportionate wing lengths (Table 2), and geographical separation of over 150 km (Fig. 3).

SPECIES DESCRIPTION.—Asterisks refer to the holotype. Characters that do not differ from those described for *L. insularis* (see Rehn and Grant 1959b:127–128) are not mentioned here. **HEAD.**

Similar in shape to that of *L. insularis*; rostrum not produced forward as in *Dracotettix*; fastigium 1.2–1.5* times as wide as long, surface lightly pitted, not rugose; occiput, gena, and subocular furrow lightly rugose. THORAX. Pronotum less rugose than in *L. insularis*, females more rugose than males; median dorsal crest distinctly elevated, but less so than in *L. insularis* (Table 2, Figs. 1e, 4b); tegmina proportionately shorter than in *L. insularis*, surpassing the apices of the hind femora by a distance less than $\frac{1}{4}$ of the total tegminal length. ABDOMEN. CONCEALED MALE GENITALIA. Endophallus (Fig. 2i) largest in the *Dracotettigini*; dorsal aedeagal valves sclerotized and short, flaring laterally with strongly serrate margins on subapical portions; ventral valves simple, with lightly sclerotized elongate lobes; sheath forming large fleshy lobes, with ventral margins extended inward to ventral cleft; epiphallus (Fig. 2j) more slender overall than in *L. insularis*; lophi with basal portion narrowly extended below and posteriorly as a slender ridge, ancora and basal ridges slender; bridge of epiphallus narrow at midsection, rather than convex as in *L. insularis*. CONCEALED FEMALE GENITALIA. Spermatheca (Fig. 4d) with apical diverticulum barely developed, even less so than in *L. insularis*, only evident before constriction to preapical diverticulum; preapical diverticulum curved several times, recurved at apex, and longer than in *L. insularis*. APPENDAGES. Hind femora with dorsal margins weakly serrate to dentate, not undulating as in *L. insularis*, hind tibiae with 9*–10 external spines and 8–9* internal spines. COLORATION. Oval mottled gray-brown, similar to coloration in *L. insularis* except pigmented with numerous small maculations rather than a few large spots and maculations, especially the tegmina with no large spots in the cubital region as found in *L. insularis*; hind wings translucent blue-green, suffused dark brown at apices; internal face of hind femora black on basal $\frac{3}{4}$ and red* or yellow-brown on distal $\frac{1}{4}$ including the genicular lobes; hind tibiae red*, yellow, brown, or gray, with brown or gray mottling on external face.

KARYOTYPE.— $2N \delta = 23$, all telocentric, two large, six medium, and three small autosomes, X medium sized. Only holotype examined, with very few meiotic divisions.

ETYMOLOGY.—From the Greek words *platy*, for flat, and *notus*, for back, in reference to the

low pronotal crest relative to that in other species in the tribe *Dracotettigini*.

TYPE DATA.—Holotype, male. Mexico. Baja California Norte: 2 km W Ejido Ignacio Zaragoza, 0.3 km E highway km marker 65 on Mex. Hwy. 3 [ca. 45 km S Tecate], 518 m, 9-III-79 (D. K. Faulkner, J. W. Brown, D. B. Weissman, DBW #79-40, SDNHM, on permanent loan to CAS, CAS Type #16484).

GEOGRAPHIC DISTRIBUTION.—Known only from the coastal mountains and Sierra San Pedro Martir of northwestern Baja California (Fig. 3).

HABITAT.—Mountainous terrain on open rocky soil with sparse grass in chaparral areas within the Californian phytogeographic region of Wiggins (1980). The type locality is a mosaic of dry summer grassland and chaparral (including *Adenostoma fasciculatum* (H. & A.), *A. sparsifolium* Torr., *Artemisia californica* Less., and *Ceanothus* spp.) on steep rocky slopes at 518 m elevation. The region consists of extensive low mountains, deeply dissected by ephemeral drainages. Both specimens from the type locality were found in the daytime on rocky soil with a sparse grass-forb cover. On the west slope of the Sierra San Pedro Martir, the two *L. platynotus* females were found in similar habitats in open areas of mixed chaparral and pine-oak woodland. One of these females was found on the ground during the day, the other was resting on the base of a *Yucca* stalk at night.

PHENOLOGY.—Adults are known from February, March, July, and September. No immatures are known.

SPECIMENS EXAMINED.—All designated paratypes. MEXICO. Baja California Norte: Sierra San Pedro Martir, west slope, ca. 680 m, 25-II-30 (Newbold, Morris, 1 ♂, ANSP); km 76.6 on road to Sierra San Pedro Martir Natl. Park off Mex. Hwy. 1, 1,500 m, 27-VII-78 (D. B. Weissman, D. C. Lightfoot, 1 ♀, CAS); km 78 on road to Sierra San Pedro Martir Natl. Park off Mex. Hwy. 1, 1,500 m, 20-IX-79 (D. C. Lightfoot, R. E. Love, J. E. Price, 1 ♀, CAS); 2 km W Ejido Ignacio Zaragoza, 0.3 km E highway km marker 65 on Mex. Hwy. 3, 518 m, late Feb. 1979 (D. K. Faulkner, J. W. Brown, 1 ♀, SDNHM).

PHYLOGENY AND DISTRIBUTION OF THE DRACOTETTIGINI

Our analysis of male internal genitalia and karyotypes confirm that *Dracotettix* and *Litoscirtus* are closely related taxa. Rehn (1938) and Rehn and Grant (1959b:134) believed that either *Litoscirtus* was “ancestral to *Dracotettix* [with *D.*

TABLE 3. Character states used in the phylogenetic analysis of the Dracotettigini.

Characters	Plesiomorphic condition	Apomorphic condition
1. Integumental sculpturing	weak (few tubercles and elevated ridges)	strong (many large tubercles and ridges)
2. Pronotal crest	low ($<0.2 \times$ pronotal width)	high ($>0.2 \times$ pronotal width)
3. Rostrum	weak ($<0.5 \times$ width)	strong ($>0.5 \times$ width)
4. Wings	long (capable of flight)	short (not able to fly)
5. Number of antennal segments	many (>20)	few (<20)
6. Form of antennae	simple (conical)	modified (flat)
7. Fastigium depressed basally	no	yes
8. Lateral margins of fastigium	complete	divided
9. Prosternal tubercle	conical	triangular
10. Subgenital plate	rounded	pointed

newboldi the intermediate link], or the two genera had a common ancestor." Rehn and Grant (1959b:129) also stated that it was not possible to determine whether *Dracotettix* or *Litoscirtus* was the older evolutionary line. We propose below a hypothetical phylogenetic history for the Dracotettigini based upon parsimony analysis (Brooks 1984).

The Dracotettigini, with five species, and Phrynotettigini, with four species, are closely related tribes (Rehn and Grant 1959b). Members of these tribes are highly specialized morphologically, with robust bodies, elaborate integumental sculpturing, and wing reduction in most taxa. The high degree of secondary specialization in external morphology renders determination of plesiomorphic vs. apomorphic character states difficult for in-group and out-group comparisons using the Phrynotettigini as an out-group. We instead used the other 14 tribes in the Romaleidae (Rehn and Grant 1959a) for out-group comparisons. A list of the character states used in our analysis of the Dracotettigini is presented in Table 3. Most of the chosen characters were considered to be useful taxonomic features for the Dracotettigini by Rehn (1938) and Rehn and Grant (1959b). Those characters are mostly secondarily derived features that also appear to be variable within populations. Discrete, conservative characters, such as genitalia and chromosome configurations, do not differ enough among taxa in the Dracotettigini to be of use in phylogenetic analyses. We used MacClade algorithms (Madison and Madison 1987) to construct phylogenetic trees, because the Dracotettigini consists of a small number of species that can readily be analyzed by an interactive program like MacClade.

The most parsimonious tree resulting from our analysis and chosen to represent our hypothesized phylogeny for the Dracotettigini is presented in Figure 5. The tree reveals that *Litoscirtus* possesses the greatest number of plesiomorphic character states, and *L. platynotus* is the most primitive taxon. *Dracotettix* forms a separate group from *Litoscirtus*, but *D. newboldi* is considerably more primitive than either *D. monstrosus* or *D. plutonius*. These findings are consistent with Rehn and Grant's (1959b) conclusions that *D. newboldi* demonstrates a relationship between the two genera. Our results indicate that *Dracotettix* is probably derived from a *Litoscirtus*-like ancestor.

The Dracotettigini is a nearctic lineage apparently derived from a neotropical ancestral romaleid (Rehn 1938). Northwestern Baja California Norte is the center of geographic distribution of the Dracotettigini, where three of the five species—*D. monstrosus*, *D. newboldi*, and *L. platynotus*—occur (Fig. 3). Of these three taxa, *D. newboldi* and *L. platynotus* are also the most primitive members of their respective genera. *Litoscirtus insularis* is a southern isolate from *L. platynotus* in the Sierra Vizcaino and adjacent offshore islands. The Sierra Vizcaino is an elevated, fog-influenced region that is biogeographically separated from the remainder of Baja California by the Vizcaino Desert. Both species of *Litoscirtus* are likely to be relictual forms of a more widespread pre-Pleistocene ancestor. During the Pleistocene, the peninsula was cooler (Savage 1960; Breckenridge 1978), and the entire Vizcaino region was probably inhabitable by *Litoscirtus*.

Dracotettix plutonius is also likely to be a relictual form of a more widespread pre-Pleisto-

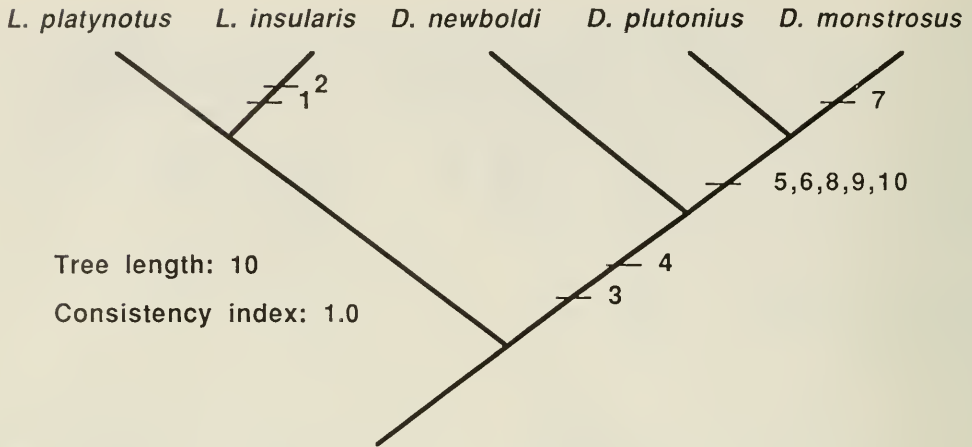


FIGURE 5. Hypothesized phylogenetic tree for the Dracotettigini based on parsimony analysis of all species in the tribe. A consistency index (Kluge and Farris 1969) of 1.0 reveals no homoplasy among characters. See Table 3 for list of characters.

cene *Dracotettix* ancestor. Suitable cooler, moister climatic conditions and associated chaparral or pinyon-juniper vegetation were prevalent across the higher elevations of the Mojave Desert during the Pleistocene (Wells and Berger 1967; Van Devender and Spaulding 1979). The ancestral form of *Dracotettix* probably dispersed east into Nevada, and populations representing *D. plutonius* apparently remained isolated in the mountains of the Mojave Desert following post-Pleistocene warming and drying trends.

The above phylogenetic and distributional scenario indicates that the Dracotettigini is an autochthonous group of species largely confined to the Mediterranean-type climatic regions of southern California and northwestern Baja California Norte. One apparent consequence of an evolutionary history in that particular climatic regime was the development of the unusual life-history pattern discussed below.

LIFE HISTORIES OF THE DRACOTETTIGINI

No species of Dracotettigini has been thoroughly studied biologically because none is found predictably in easily accessible locations. With the exceptions of the 1917-18 Nellie population of *D. monstrosus* in San Diego County, California (see below), and *L. insularis* population on Cedros Island, Baja California Norte, individuals of Dracotettigini have been rarely encountered. Long-term studies spanning several years and using marked individuals are needed to completely understand life history and reproductive

strategies and to ascertain which reproductive properties are truly facultative. Nevertheless, piecemeal data are available, especially in Rehn and Grant (1959b), although those authors did not attempt to construct a hypothetical life cycle. We do so here for *D. monstrosus*, based on literature, museum and field dissections, our laboratory rearings, and certain caveats, as indicated below.

Adult female *D. monstrosus* utilize a summer reproductive dormancy period, depending upon local thermal and precipitation regimes. Most females in most populations become adult in late winter or early spring. Those at low elevations in dry, hot southern California pass the spring, summer, and early fall periods unmated and reproductively inactive. Although not proven, they apparently mate and oviposit many months after becoming adults, with the advent of fall and winter rains. They then lay eggs that probably have no dormancy period. In contrast, most females living at higher, cooler, wetter localities in San Diego County mate and oviposit shortly after becoming adults in the spring and subsequently die (see below). Their eggs probably have no dormancy period. Some females (see Table 4) from these same high-elevation San Diego populations do not become adults until summer. We predict that they enter reproductive dormancy unmated and remain reproductively inactive until fall and winter rains arrive. In northern California mating pairs of *D. monstrosus* are known from April (Strohecker et al. 1968) and June (Rehn and Grant 1959b), indicating a life cycle

TABLE 4. Seasonal data for *Dracotettix monstrosus* collected in Nellie, San Diego County, California, from 1917-18.

Life stage	Numbers of individuals/month collected				
	April	May	June	July	August
Adult ♂	24	0	7	1	12
Adult ♀	14	4	0	2	1
Adult ♀ with eggs	9*	4	0	2	1
Last instar	0	0	0	2	29
Penultimate instar	0	0	0	7	12

* Three of five without eggs had previously oviposited.

similar to spring adult females at higher elevations in San Diego County. Small nymphs have been collected in June from Santa Clara County, California (Rehn and Grant 1959b), indicating no egg dormancy.

We now report that adult females of all five species of the tribe Dracotettigini can become reproductively inactive during extended hot, dry periods. Unfortunately, we do not know if four of these species have the interpopulation reproductive plasticity seen in *D. monstrosus*. The above scheme contrasts with that used by most grasshoppers inhabiting California's Mediterranean climatic zone. Individuals of these latter taxa pass the winter in egg or early instar dormancy and become adult in late spring or early summer, mate, oviposit, and die in four to six weeks (pers. obs.).

METHODS

FEMALE MATING STATUS.—Spermathecae of adult females of all five species were examined for the presence of sperm according to Weissman (1979). We could not find dried spermatophores, as did Whitman and Orsak (1985).

FEMALE EGG MATURATION STATUS.—Terminology employed is that of Weissman and French (1980). Individuals that we collected were dissected shortly after death and examined for the presence of eggs, whereas museum specimens were dissected after their abdomens were placed in boiling water for one to two minutes. Field-captured adult females were considered reproductively dormant if they were nonteneral with extensive fat reserves and no ovarian development. Such reproductively dormant females were physically active, had full crops, and may or may not have been mated.

FEMALE OVIPOSITION STATUS.—Museum females that were obviously reproductively active

(i.e., contained mature eggs) died with their ovipositor valves open, an observation previously made by Phipps for females killed with chloroform (1962) or cyanide (in litt., J. Phipps to D. B. Weissman 1986). Open ovipositor valves were seen when ovaries showed some development (i.e., Stage III of Phipps 1966), but was absent in some species (Phipps 1970).

Phipps (1966) discussed the three certain criteria of ovulation: (1) presence of eggs in the oviducts; (2) presence of traces of foam on the ovipositor valves; and (3) presence of egg resorption bodies. Criteria (1) and (2) are applicable to museum specimens, but we found (2) to be unreliable in the Dracotettigini. The absence of foam as a reliable indicator for the lack of prior oviposition is critical only for those females captured during reproductive dormancy, as reproductively active females would have eggs on dissection. We found museum specimens of *D. monstrosus* females that were obviously reproductively active before death, with ovulated eggs and gaping ovipositor valves, but no apparent traces of foam. Additionally, we have examined known laboratory-ovipositing females and found no traces of foam.

RESULTS

Dracotettix monstrosus. The most extensive natural history data are known for this species. The largest sample examined was 115 individuals collected during 1917-18 by E. P. Hewitt from Nellie, San Diego County, California, elevation 1,630 m, and borrowed from ANSP. A summary of these individuals by age, sex, and collection dates is presented in Table 4. All 21 adult females were dissected; 16 had mature eggs, including the three collected in July and August. The five without eggs were collected in April; three of these had dried foam between their ovi-

TABLE 5. Life history data for *Dracotettix monstrosus* (data from text and Rehn and Grant 1959b). X—known records; X'—known records, high-elevation localities (e.g., Nellie, Table 4); ?—hypothesized occurrences.

Stage	Month											
	J	F	M	A	M	J	J	A	S	O	N	D
Nymphs	?	?	?	?	?	X	X	X	X	?	?	?
Adults	?	X	X	X	X	X	X	X	X	X	?	?
Oviposition	?	X	X	X	X	X'	X'	X'		?	?	?
Female reproductive dormancy					X	X	X	X	X			

positor valves, indicating prior oviposition. The San Diego region had received good winter precipitation during the 1916–18 period (U.S. Department of Commerce 1916–18).

Seven individuals of *D. monstrosus* collected by D. K. Faulkner in Pine Valley (ca. 1,100 m elevation), San Diego County, California, late April 1979, were kept in the laboratory at room temperature and exposed to natural day length. The three females were gravid when collected and copulated with the males. These females oviposited in mid-May and died soon after, indicating that spring-ovipositing females probably do not live through the summer. Two of the four males survived until mid-November. In the field such long-lived males may fertilize those females that become adult during the summer (see Table 5) and remain reproductively inactive until fall, when they mate and oviposit. Unfortunately, no eggs hatched over the next year under conditions that result in hatching of other sympatric grasshopper species. Three additional females were collected at lower elevations in more arid regions of southern California in late July 1971 and mid-August 1973. None of these females had mated or had eggs, in contrast to the three reproductively active summer females from Nellie (Table 4 and above). Two males collected in northern Baja California Norte (mid-May 1979) and Los Angeles County (late June 1971) had abundant testicular meiotic division. We do not know if such males are sexually active.

Dracotettix newboldi. One non-teneral female collected in early July 1978 was unmated and without egg development. The presence of adults in February (the types) and July indicates a life history similar to that of *D. monstrosus*.

Dracotettix plutonius. The presence of adults from March to October (Rehn and Grant 1959b; Barnum 1964; and our observations) indicates a life history similar to that of *D. monstrosus*.

Litoscirtus insularis. In early April 1983, many adults and late instar nymphs were present on

Cedros Island, Baja California Norte. Of three females dissected, none had ovarian development. Mating status was not determined. By early July 1983, many adults, but only two last instar nymphs, were found. Of 10 females examined, none had ovarian development, although three were mated. July males had abundant testicular division. We attempted to return to Cedros Island in September 1983, but torrential storms on Cedros prevented us. We did return to Cedros Island in late September 1984, but no individuals were found despite intensive searching. We suspect that adults were aestivating in sheltered areas awaiting fall rains that would induce reproductive activity. One of two females collected on the adjacent Baja peninsula in February 1973 had mature eggs.

Litoscirtus platynotus. Two nonteneral females collected in July 1978 and September 1979 were unmated and without eggs. The holotype male collected in early March 1979 had few meiotic divisions, but large amounts of mature sperm.

POSTULATED LIFE CYCLE OF *DRACOTETTIX MONSTROSUS*

1. Adults of both sexes and late-instar nymphs overwinter, as indicated by their appearance in late winter and early spring (see Table 5).

2. Most females from northern latitudes or high-elevation, cool, moist, southern localities mate in spring, have a period of oviposition, and die after a few months. Eggs laid in spring in central California hatch without a dormancy as indicated by the appearance of mating pairs in spring and early instars in June (Rehn and Grant 1959b).

3. Females from low-elevation, hot, dry southern localities similarly become adults in spring, but subsequently enter summer reproductive dormancy, most or all without mating. Eggs laid in fall and winter by these females apparently hatch over several months because of

cool temperatures, coupled with a long oviposition period. This accounts for the late-instar nymphs collected in spring. These adult females will be long lived, a condition found in other grasshoppers that utilize a reproductive dormancy (Uvarov 1966b; Weissman 1979; Weissman and French 1980; Rentz and Weissman 1981).

Those few females that mate in late spring and then become sexually dormant will have sperm in their spermathecae during their summer dormancy (a condition documented in *L. insularis*, but only postulated for *D. monstrosus*). The energy expenditure needed to keep these sperm alive through the summer (see similar example in LeCato and Pienkowski 1973) may be reproductively less expensive than relying on the presence of males to effect copulation in the fall, although male *D. monstrosus* can survive for seven months in the laboratory (see above). Similarly, females of the Egyptian locust store sperm during their six-month winter dormancy period between mating and oviposition (Uvarov 1966a).

4. Adult males of species whose synchronic females are in reproductive dormancy are probably never completely reproductively inactive. They usually have some meiotic divisions, even during the summer when they accumulate sperm prior to fall mating activity. It is unknown if males are sexually receptive when females are in dormancy.

Temporal aspects of the above scheme for *D. monstrosus* probably also apply to the other species of Dracotettigini, except *L. insularis*, since these four taxa all inhabit a region with similar rainfall periodicity, and all apparently have the ability to pass the summer in dormancy. The overall pattern for *L. insularis* is similar. The actual timing is different in that some females become adult in the fall and winter, mate, oviposit, and soon die. Those females becoming adult later in late winter or early spring may mate but all pass the spring and early summer reproductively dormant. These females probably become reproductively active whenever significant precipitation arrives. Such rainfall comes earlier in the year (July to January) in the central region of Baja California than farther north (October to May) in northern Baja California Norte and southern California.

SOME UNANSWERED QUESTIONS

Because of yearly fluctuations in population size of most species of Dracotettigini and our

inability to simply find any individuals of certain species, parts of this study were intellectually unsatisfactory. Some gaps in our knowledge have already been referred to within the text. Entomologists in the future will unpredictably encounter populations of Dracotettigini species. To optimize such occasions, we list some questions that we attempted to answer, but could not. We concentrate on *D. monstrosus* because it is the most common and geographically widespread, and best studied of the Dracotettigini.

1. What percentage of *D. monstrosus* females overwinter as adults, and what percentage utilize a reproductive dormancy? A mark-release-recapture study (e.g., Weissman and French 1980) will probably be necessary to answer this and several other questions below.

2. How reproductively plastic are the individuals in each population of each species, since precipitation patterns in Mediterranean type climates are highly variable?

3. Is it possible that certain high-elevation females oviposit in the spring, become reproductively dormant during the summer, and oviposit again in the fall? It is known that males of the grasshopper species *Oedipoda miniata* (Pallas) with a reproductive dormancy can have these cycles reversed by appropriate changes in laboratory photoperiod and temperature (Pener and Orshan 1980). Could this reversal occur in field populations of *D. monstrosus*? Phipps (in litt. to D. B. Weissman 1986) was not aware of any African species of grasshopper, of which up to 70% of taxa utilize a reproductive dormancy during the dry season, that appeared to have oviposited and later entered reproductive dormancy.

4. Do male *D. monstrosus* from low-elevation localities employ any form of reproductive dormancy, such as reduced rate of meiosis, reduced sexual receptivity, or reduced activity level?

5. Do the eggs of *D. monstrosus* have a facultative dormancy?

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